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SUCKLING BEHAVIOR IN DOMESTIC GOATS: INTERACTION BETWEEN LITTER SIZE AND KID SEX

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ABSTRACT: Studies of milk allocation in polytocous species provide the opportunity to investigate the effects of offspring number and sex ratio on maternal investment. In these species maternal control over milk allocation is more difficult because physiological limits on milk production may stimulate sibling competition. This study investigated the nursing behavior of domestic goats bearing twins or singletons in an experimental situation for the first 47 days post-partum. Milk yield and composition did not correlate with litter size, kid weight, or with the behavior of kids. Males were heavier than females, but there were no sex differences in behaviors related to nursing. Milk allocation differences existed between twins and singletons, even though, on the average, there were no significant weight differences. However, one twin was always larger than the other. Twins spent less time in proximity to the mother than did the singletons, and were more responsible for achieving proximity to the mother. These results suggest that nursing behavior was more affected by litter size than by sex of young, although there might be an interaction between both, that early mother-young interactions were different for twins and singletons, and that kids played an active role in the allocation of milk and its conversion to body weight.

Infant mammals are entirely dependent on milk to meet their nutritional needs during early development; milk consumption is directly related to infant growth, and milk is the conduit for the transfer

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of proteins necessary for the development of an immune system (Jenness, 1986). Therefore, infants and juveniles should strive to acquire as much of this essential resource as possible, and mothers should distribute it in a manner that increases their own reproductive success, both immediate and future (Trivers, 1974; Wilson, 1975). Since the genetic self-interests of mother and offspring are not necessarily congruent (Trivers, 1974), and young differ in reproductive value and needs (Mock & Forbes, 1992), milk allocation provides a rich context for parent-offspring conflict. Studies of parental care have been concerned with how resource allocation to progeny is biased by offspring sex and litter size (Winkler & Wilkinson, 1988), but few studies consider the interaction between both (Gaillard, Pointier, Brandt, Jullich, & Allaine, 1992; Soderquist, 1995).

For polygynous mammals, evolutionary theory predicts that mothers should bias milk allocation toward sons if (1) maternal provisioning is positively related to offspring size at maturity and (2) increased maternal provisioning has a more pronounced effect on the fitness of sons than of daughters (Byers & Bekoff, 1990; Maynard Smith, 1980; Trivers, 1972). This might plausibly occur in species in which adult size is influenced by access to food during early development and in which larger males enjoy a competitive advantage over smaller males in obtaining mates. Although some studies have documented that male offspring receive a greater investment of maternal resources than female offspring (see reviews by Byers & Bekoff, 1990; Clutton-Brock, 1991), Byers and Bekoff (1990) argued that whether the mother or offspring control resource allocation has not been demonstrated adequately. This demonstration is needed to understand the extent to which natural selection operates on maternal and infant traits. A complete understanding of the mechanisms of milk allocation requires investigation of the dynamics of parent-offspring interactions, especially the role of the young in mediating the distribution of milk.

Ungulates present an excellent opportunity to test these theoretical predictions, because they show a wide range of polygyny, sexual dimorphism, and males fight for access to females (Jarman, 1983); and because the young, although precocial in comparison to most other mammals, are dependent on milk for the first three or four months of life. Male-biased milk allocation has been described in bison (*Bison bison*), horses (*Equus caballus*), and red deer (*Cervus elaphus*), but not in cattle (*Bos* sp.), bighorn sheep (*Ovis canadensis*), white tail deer (*Odocoileus virginianus*), and fallow deer (*Dama dama*), for example

(reviewed by Byers & Bekoff, 1990; Clutton-Brock, 1991). In some polytocous species, such as pronghorn (*Antilocapra americana*), female offspring seem to suckle more than males (Byers & Moodie, 1990). In species with high growth rates, mothers might be near the upper limits of milk production and may not be able to provide enough extra milk to support differential investment in any one sex (Byers & Moodie, 1990).

Although studies of sex-biased milk allocation in ungulates have focused on species bearing single offspring, polytocous species provide the opportunity to investigate the effects of offspring number and sex ratio on milk allocation. In these species maternal control over milk allocation is more difficult because physiological limits on milk production may stimulate competition between siblings. Reduced suckling frequencies and/or growth rates in twins relative to singletons have been reported in domestic sheep (Ewbank, 1965, 1967) and cattle (Price, Martinez, & Coe, 1984/85), suggesting that sibling competition might be expected. However, the litter size effect was not present in pronghorn antelope for nursing frequency (Byers and Moody, 1990). Since sibling competition can reduce the fitness of parents (Godfray & Parker, 1992), mothers might be expected to buffer sibling interactions (Pianka, 1988) or to favour offspring most likely to increase her inclusive fitness (Maynard Smith, 1980). For example, in the first two hours after parturition, domestic goat mothers provide more nursing to the smaller, less vigorous kid, and these compensation efforts correlate with the dominance status of these kids (Klopfer & Klopfer, 1977; Klopfer & Klopfer, 1973). Thus, studies of milk allocation in polytocous species should consider, in addition to sex-biased milk allocation, the dynamics of nursing several young versus one, and whether the mother buffers or encourages sibling competition. Furthermore, different litter sizes represent different social environments, and thus a context to study alternative behaviors used by the young in the procurement of resources.

In this study we investigated the nursing behavior of domestic goats bearing twins or singletons in an experimental situation for the first 47 days post-partum. Our objectives were to evaluate whether the expected sex-biased milk allocation was evident in either singletons or twin litters, to ascertain the role of the young in the allocation of milk, and to determine the extent to which litter size affects mother-young interactions. Subsidiary goals were to characterize sibling competition and observe whether mothers mediated competitive interactions among siblings. Domestic goats are a particularly appropriate model for studying the dynamics of nursing interactions because they are highly

tractable, produce up to four offspring per litter, and mother-young interactions are fairly well characterized. Also, for dairy breeds it is unlikely for differential investment to be limited by milk availability. This provides a convenient context in which to examine the relative roles of mother and infant in controlling access to maternal resources.

METHOD

Subjects

This study was conducted at the Dairy Goat Research Facility of the University of California at Davis. The study group consisted of 18 adult female Alpine-breed goats between 2 and 3 years of age and their 26 offspring. Several subjects were eliminated from the study because of illness, therefore only the behavioral and growth data from 16 does and 22 kids are presented here: 6 sets of twins (4 male-female, 1 male-male, 1 female-female) and 10 singletons (5 males and 5 females). Milk composition data were collected for 16 of the does. All adult goats had given birth once previously, but this was the first time that they were allowed to raise kids. The mean body height at the shoulder for adult does was 72.17 cm ($SD=3.38$) and the mean body weight was 47.19 kg ($SD = 6.89$). All subjects were housed in a 33.2 x 7.4 m corral with an elevated wooden shed for shelter. Hay and grain were provided *ad libitum* once a day. The does were allowed to nurse their kids *ad libitum* during non-test days, but on test-days they were allowed to nurse their kids only during the observation time.

Procedure

The objective was to structure mother-offspring reunions so that we could observe nursing dynamics under conditions in which mother and offspring were motivated to engage in the interaction. The kids were observed at around 5, 12, 19, 26, 33, 40, and 47 days of age. Kids were artificially weaned at 52 days of age. At each age, three observation sessions were done between 7 and 10 am, and three between 7 and 9 pm. Kids were separated from their mothers around 10pm the night before each of the morning observations and around 10:30 am before the afternoon observations. These procedures were not different from normal husbandry procedures at the Dairy Goat facility. These separation times are not unusual for domestic animals and are within

the range seen for feral goats (Coblentz, 1974; O'Brien, 1984; Ruiz-Miranda & Chabert, 1989). Because births were not completely synchronous, only between 4 and 6 kids were tested simultaneously.

The focal units were the mother and her one or two kids, and were observed for a minimum of 45 minutes and a maximum of 90 minutes. The time differences depended on the visibility of subjects, and unpredictable environmental factors. Before reintroducing the mothers to the home corral containing the rest of the females and their kids, we confined the kids behind a shed, releasing them only after their mothers entered the corral. All occurrences sampling (Martin & Bateson, 1986) was used to record nursing and approaches and leaves, and 5-minute interval sampling was used to record distance between kid and mother, and the behavior of kids. Behavioral variables analyzed were:

1. *Proximity to the Mother.* The number of intervals spent at distances of 2 meters or less from the mother were grouped under the label "Proximity".

2. *Kid Behavior.* Resting: Lying down alone or with its sibling in a covered area for more than 15 seconds. Feeding: Mouthing or chewing anything that was not milk or part of the corral furniture. Ruminating was also included here. Other: Any behavior that did not fit into one of the preceding categories.

3. *Approaches and Leaves.* We recorded the initiator and frequency of approaches (a distance change from more than 1 meter to within a meter of the target animal), or leaves (move away to a point further than one meter from target animal) between mother and offspring.

4. *Nursing.* A nursing bout (i.e., a nursing event) was defined as the kid suckling for 5 seconds or more with no interruptions longer than 5 seconds. For analysis, the total number of bouts was divided by the total observation time to calculate the Nursing Bout Rate. Bout Length was defined as the mean of the durations of all nursing bouts. Time Nursing was defined as the sum of the durations of all nursing bouts divided by the total observation time. In addition, for each nursing bout we recorded which kid nursed first, which kid was the displacer (see below), and the dam's behavior. A displacer was any kid that approached from the same side as the nursing kid and pushed the nursing kid off the nipple that it was suckling, thereby forcing it to use the other nipple or abandoning nursing completely. The behavior of the dam was recorded as Presentations (any behavior done by the mother that resulted in a kid being closer to the udder as opposed to the face of the mother) or Withdrawals (any behavior that resulted in the kid being

farther away from the udder). Withdrawals and Presentations took the form of licking or butting or walking a few steps or turning around. These behaviors were interpreted to be a solicitation or encouragement to nurse.

6. *Nursing Failures*. Attempts at nursing that were rejected by the mother and were less than 5 seconds long. An attempt to nurse was defined as either touching the udder or getting within six inches from it with the apparent intention to nurse.

6. *Nursing Success*. This was calculated for each kid by dividing the total number of nursing bouts by the sum of nursing bouts and nursing attempts.

7. *Milk Stealing*. All nursing failures and successful nursings made by kids other than the offspring of the focal mother, and all attempts that the focal kids made to nurse from mothers other than their own.

8. *Milk Yield and Composition*. The Dairy Goat Facility performed a standard analysis of the milk of each adult female once: when their kids were 52 days old. A timed-milking (Ofstedal, 1984) procedure was used to collect the milk. The milk composition data included the complete morning and afternoon milkings of one day. Two measures are reported here: quantity (yield in pounds) and fat content (in pounds).

Statistical Analyses

Twins were treated as statistically independent from each other, because their scores on most variables were not correlated. Also, previous studies with goats found that intra-litter variation in behavior is as large as inter-litter variation (Klopfer & Klopfer, 1977; Ruiz-Miranda, 1992). For the statistical analyses of sex and litter size differences of all variables, except body weight, the data for each individual were averaged across ages into first and second month. This grouping was done to maintain sample sizes because some kids were not observed at all ages because they were sick or their mothers had mastitis. The analyses of the effects of body weight, growth, and age on nursing and proximity to the mother used weekly data points. Overall tests of significance were done with Repeated Measures ANOVA using SYSTAT (Wilkinson, Hill, & Vang, 1992), and for post-hoc comparisons we used one-way ANOVA. Correlations were calculated with Pearson's Product-Moment test. Continuous variables were normalized with Log transformation and frequencies variables

were normalized using a Square Root transformation. Significant p values were at $p < 0.05$.

RESULTS

Maternal Variables

The only significant correlations were between milk yield and maternal age ($r = .83$, $p = 0.0001$) and maternal weight ($r = .87$, $p = 0.0001$). The difference in Milk Yield between does with twins (Mean = 8.62, SD = 2.05) and singletons (Mean = 9.11, SD = 2.89) was not statistically significant ($F(1,14) = .16$, $p = 0.69$). There was no significant weight difference between does with twins and does with singletons ($F(1,15) = .001$, $p = 0.91$). Milk Yield was found to be moderately correlated with Time Nursing at 47 days ($r = .57$, $p = 0.02$), but weakly correlated to Kid Weight at 47 days ($r = .36$, $p = 0.17$). Therefore, although larger goats tended to produce more milk, this did not affect nursing and growth of kids in any systematic way.

Age of Kid

Kid age had a significant effect on all nursing behavior measures. Time spent nursing declined with age ($F(6,15) = 7.38$, $p = 0.0001$), as did the length of individual nursing bouts ($F(6,15) = 2.92$, $p = 0.03$). Nursing success significantly declined with age ($F(6,15) = 1.83$, $p = 0.04$), and the number of nursing attempts increased with age ($F(6,15) = 2.71$, $p = 0.002$). The frequency of milk stealing was higher during the second month (Mean = 2.92; SD = 0.62) than during the first month (Mean = 0.82; SD = 1.33), with a peak at 33 days of age ($F(1,15) = 4.76$, $p = 0.04$).

The kid's age also had a significant effect on doe-kid association measures. As kids got older they initiated more of the approaches ($F(6,15) = 7.08$, $p < 0.001$); kids initiated more than 50% of the approaches after 12 days of age. Moreover, kids spent more time in proximity to their mothers as they got older ($F(6,15) = 2.34$, $p = 0.04$), at least until 40 days of age.

Sex of Kids

Body weight and growth. Males tended to be heavier than females

at all ages (Figure 1a, $F(1,20) = 6.36, p=0.02$). Weight gain was also higher for males than for females ($F(1,20) = 4.02, p = 0.05$).

Nursing behavior. There were no sex differences in time nursing (Table 1, $F(1,20) = 0.61, p = 0.44$), even though males had longer mean bout length than females (Table 1, $F(1,20) = 5.02, p = 0.04$), particularly during the first month of life. Males and females did not differ in nursing success ($F(1,20) = .64, p = 0.43$). Both the rate of nursing attempts and the nursing success (Table 2) of males and females were similar throughout the study ($F(1,20) = 0.01, p = 0.92$; and $F(1,20) = 0.55, p = 0.47$, respectively). When attempts to nurse from non-maternal does (milk stealing) were considered we found that out of 47 successful steals, 33 were made by males and 14 by females. Milk stealing was observed in 7 males and 5 females, and one of the males was responsible for 18 of the milk steals (38.3 %). Differences between the sexes in the frequency of udder presentations by the mother for both twins and singletons were not statistically significant.

Table 1. Monthly average for the proportion of time spent nursing and length of individual nursing bouts (seconds) for males and females born as singletons or twins. Month 1 = 5 to 26 days old; and Month 2= 33 to 47 days old. Numbers in parentheses are the standard deviations.

		Month 1			Month 2		
		Single	Twin	All	Single	Twin	All
Time Nursing	Male	.157 (.06)	.084 (.03)	.117 (.06)	.091 (.05)	.041 (.01)	.063 (.04)
	Female	.116 (.05)	.086 (.03)	.10 (.04)	.058 (.02)	.050 (.03)	.055 (.03)
	All	.137 (.05)	.085 (.03)	.109 (.05)	.074 (.04)	.046 (.02)	.059 (.04)
	Male	87.49 (31.1)	63.26 (28.4)	75.38 (29.7)	48.92 (24.7)	36.46 (9.6)	42.69 (17.1)
	Female	52.34 (15.2)	47.72 (19.3)	50.03 (17.2)	35.01 (4.8)	35.71 (11.8)	35.36 (8.3)
	All	69.92 (29.6)	55.49 (24.5)	62.71 (27.0)	41.96 (18.3)	36.08 (10.3)	39.02 (14.3)

Table 2. Monthly averages for Nursing Attempts (successful + unsuccessful/ time) and Nursing Success (successful attempts/ total number of attempts) for male and female kids born as singletons or twins. Month 1 = 5 to 26 days old; and Month 2= 33 to 47 days old. Numbers in parentheses are the standard deviations.

		Month 1			Month 2		
		Single	Twin	All	Single	Twin	All
Nursing Attempts	Male	.05 (.02)	.223 (.11)	.145 (.12)	.197 (.09)	.296 (.20)	.251 (.16)
	Female	.09 (.02)	.149 (.09)	.122 (.08)	.251 (.21)	.274 (.14)	.264 (.17)
	All	.071 (.03)	.186 (.11)	.134 (.09)	.224 (.16)	.285 (.17)	.257 (.16)
Nursing Success	Male	.723 (.12)	.378 (.12)	.535 (.21)	.423 (.19)	.275 (.17)	.342 (.19)
	Female	.676 (.05)	.563 (.10)	.614 (.10)	.416 (.25)	.313 (.13)	.360 (.19)
	All	.699 (.09)	.471 (.14)	.575 (.17)	.419 (.21)	.294 (.15)	.35 (.19)

Approaches and proximity to the mother. There were no statistically significant differences between males (Mean for month 1 = 0.59, SD = 0.14; Mean for month 2 = 0.81, SD = 0.08) and females (mean for month 1 = 0.62, SD = 0.19; Mean for month 2 = 0.79, SD = 0.05) for the proportion of approaches initiated by the kids ($F(1,20) = 0.02, p = 0.90$). The differences between males (Mean for month 1 = 0.55, SD = 0.26; mean for month 2 = 0.44, SD = 0.21) and females (Mean for month 1 = 0.59, SD = 0.25; Mean for month 2 = 0.52, SD = 0.19) for the time in proximity to the mother were also not statistically significant ($F(1,20) = 0.61, p = 0.44$).

Other behavioral differences. Behavioral differences related to energy acquisition and expenditure did not explain the differences in body weight and growth between the sexes. Time spent resting was similar for males (Mean = 0.32 s, SD = 0.12) and females (Mean = 0.29 s; SD = 0.10; $F(1,20) = 0.58, p = 0.45$). The differences between the males (Mean = 0.10 s, SD = 0.06) and females (Mean = 0.09 s, SD = 0.03) in amount of time spent foraging were not statistically significant ($F(1,20) = 0.54, p = 0.47$).

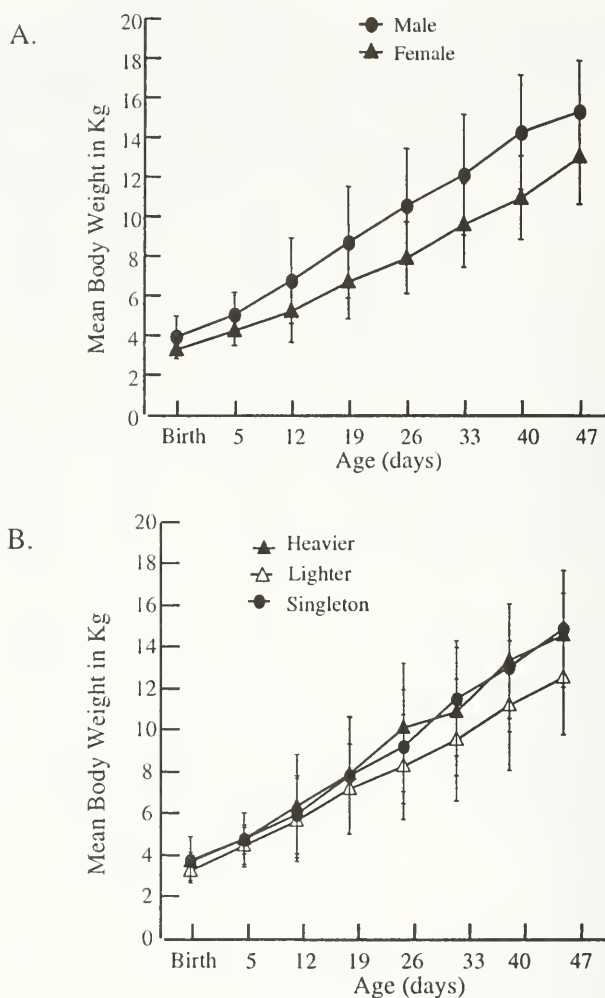


Figure 1. Body weight (mean and standard error) of A. Male and female kids from birth to 47 days of age, and B. Singleton and twin kids from birth to 47 days of age. Data from the twin kids is divided according to relative weight category.

Twins versus Singletons

Body weights and growth. The relationship between body weight and litter size was more complex than the effect of kid gender. Overall, the differences between twins and singletons in body weight (Figure 1b) and growth were not statistically significant (Weight: $F(1,20) =$

0.32, $p = 0.57$; Growth: $F(1,20) = 1.52, p = 0.23$). However, one of the twins tended to be heavier than the other (Figure 1b). All twin pairs showed the light-heavy relationship, and in the the mixed sex pairs the heavy twins were the males (Table 3). The average weight for heavier twins was equal or higher than that of singletons, whereas the average weight of the lighter twins was always lower than the one of singletons.

Nursing Behavior. Singletons did not differ from twins in duration of individual nursing bouts ($F(1,20) = 1.84, p = 0.19$), but nursed more frequently ($F(1,20) = 4.4, p = 0.05$), resulting in a greater time spent time nursing (see Table 1; $F(1,20) = 7.41, p = 0.01$). Nursing success (Table 2) was significantly higher for singletons than for twins ($F(1,18) = 11.31, p = 0.003$). These differences were not caused by a lack of effort from the twins; the rate of nursing attempts (Table 2) was higher for twins than for singletons throughout the study ($F(1,20) = 3.72, p = 0.06$). When attempts to nurse from does other than the mother (milk stealing) were considered we found that out of 47 successful steals, 39 were done by twins and 8 by singletons. Out of the 12 kids involved in milk steals 8 were twins and 4 were singletons, and one twin was responsible for 18 of the steals (38.3 %).

Table 3. Actual body weight (Kg) growth rate (Kg/day), proportion of times subject displaced sibling from udder (Displacer) and classification into weight categories for each kid in a twin pair. Adjacent kids in the table are siblings.

Kid ID	Mother ID	Sex of Kid	Birth Wt	Weight Month 1	Weight Month 2	Growth Rate	Weight Category	Dis-placer
0024	8054	Female	3.4	11.34	14.60	.25	Lighter	.18
0025	8054	Male	4.2	14.97	16.87	.29	Heavier	.82
0028	9046	Male	4.0	12.24	15.87	.25	Heavier	.33
0029	9046	Male	3.6	11.34	14.97	.24	Lighter	.67
0040	9034	Male	3.2	10.34	13.15	.21	Heavier	.91
0041	9034	Female	2.7	6.80	10.43	.16	Lighter	.09
0046	9065	Female	3.4	7.71	14.87	.24	Same	.45
0047	9065	Female	3.5	8.62	14.97	.24	Same	.55
0074	9070	Female	2.6	5.44	9.25	.14	Lighter	.14
0075	9070	Male	3.1	6.80	12.24	.19	Heavier	.86
0078	6035	Female	3.7	6.8	10.43	.14	Lighter	.00
0079	6035	Male	4.0	7.71	13.15	.19	Heavier	1.00

Litter size did not have a significant effect on the frequency of mothers presenting their udders to kids ($F(1,20) = 2.65, p = 0.11$). The trend was, however, for singletons (Mean for month 1 = 20.70, SD = 14.10; Mean for month 2 = 3.80, SD = 4.49) to receive more udder presentations than twins during both months (Mean for month 1 = 14.17, SD = 12.15; Mean for month 2 = 1.0, SD = 1.35). Variation among each group was high and probably accounts for the lack of significance.

Competition and displacements. With twins pairs it was possible to look at sibling competition for udder access by recording the number and pattern of displacements from the teats. We emphasized two variables, body weight and sex (Table 3). The overall main effect of sex was statistically significant ($F(1,6) = 8.82, p = 0.02$), with males displacing females more often than the opposite. Body size had a significant main effect in both mixed sex and single sex twin pairs. The Heavy kids displaced their twins more often than the reverse ($F(1,10) = 17.22, p = 0.002$). Differences between Heavy and Light twins in Time Nursing were not statistically significant ($F(1,10) = .15, p = 0.70$).

Approaches and proximity. Even though the overall effect of litter size was not statistically significant ($F(1,20) = 2.73, p = 0.11$), twins (Mean = 0.67, SD = 0.15) initiated more approaches than singletons (Mean = 0.53, SD = 0.16) during the first month ($F(1,20) = 4.79, p = 0.04$). Singletons (Mean for month 1 = 0.67, SD = 0.22; Mean for month 2 = 0.58, SD = 0.16) spent significantly more time in proximity to their mothers than twins (Mean for month 1 = 0.48, SD = 0.25; Mean for month 2 = 0.39, SD = 0.19) throughout the study ($F(1,20) = 7.07, p = 0.02$).

Resting and foraging. The difference in resting behavior between singletons (Mean = 0.32; SD = 0.59) and twins (Mean = 0.29; SD = 0.64) was not statistically significant ($F(1,20) = 1.2, p = 0.28$). The differences between singletons and twins in amount of time spent foraging were not statistically significant ($F(1,20) = 2.54, p = 0.12$).

DISCUSSION

Milk allocation was more affected by litter size than by sex of young, although there might be an interaction between both factors, kids played an active role in the allocation of milk and its conversion to body weight, and early mother-young interactions were different for

twins and singletons. The relationships between age of kid and behavioral variables follow the same patterns seen in field studies of wild bovids (Byers & Moodie, 1990; Green, 1992; Hass, 1990; Schaller, 1977), and more naturalistic studies of domestic ruminants (Ewbank, 1967; Lickliter, 1984, 1987; Mandiki, Fossion, & Paquay, 1989; Peña Blanco, Herrera García, Subires Antúnez, & Aparicio Macarro, 1985; Reinhardt & Reinhardt, 1981).

Resource Allocation

We found that males were heavier than females from birth to day 47. One might expect then that males had more access to post-natal resources from the mother, but that was not true for time nursing, nursing success, and nursing attempts. Other domestic bovids show this pattern of sex differences in size but no sex differences in nursing behavior (Burfening, 1972; Plasse, 1978; Reinhardt & Reinhardt, 1981). So, how do males grow larger than females? It is possible that male kids obtained more milk per unit time. Males had a longer nursing bout length than females, and this can result in higher milk (or milk fat) per unit of time, especially if the first few seconds of suckling are "dry" compared to the last few seconds (Ofstedal, 1985). However, available data shows that there are no sex differences in milk consumed in hand reared kids fed milk ad-libitum (Hadjipanayiotou, 1986) or twice per day (Peña Blanco, et al., 1985). Males could be more efficient at converting milk into body weight than females, but there are no data to test this alternative. It is also possible that males procured milk or other nutrients elsewhere or that males had different activity budgets than females. The only data germane to this hypothesis is the slight male bias in milk stealing observed. All of these alternative explanations suggest that to explain growth differences between sexes we should be looking at physiological and behavioral traits of kids, as well as at female resource allocation.

Being a twin or a singleton had a significant effect on milk allocation and interactions with the mother, but not on body weight. On average, twins did not differ from singletons in body weight, although among twin pairs there was always a smaller twin which weighed less than singletons. Although the weight differences among twins can be partially explained by the sex differences (4 of 6 pairs were of mixed sex), the differences were also present in same sex pairs (one male-male and one female-female). A study with larger sample size is necessary to corroborate our observations. Singletons were more

successful in their solicitations, nursed longer, and spent more time in proximity to their mothers than twins. Also, mothers with singletons sought their kids more often than mothers with twins, and stayed closer to them. Differences in nursing behavior were surprising since dairy goats are thought to produce enough excess milk to feed several kids. However, in this study does with twins did not produce twice the amount of milk than those with singletons, and thus milk supply was more limited for twins.

The lack of a strong litter size effect on body weight is in contrast with studies carried out on 'meat' goat breeds and other domestic bovids. In meat goats, singletons obtained more milk and gain more weight than twins (Figueiredo, Simplicio, Bellaver, & Pant, 1982; Hadjipanayiotou, 1986). Meat goats are smaller and produce less milk (mean=4.26 (.33) kg/goat/day) than the dairy goats used here (5.31 (.20) kg/goat/day). Milk is in more limited supply for twin meat goats than for twin dairy goats. Singletons were heavier than twins at all ages in Clun Forest and Texel sheep, even though twins had longer suckling bouts and higher total duration of suckling than singletons during the first 5 weeks of lactation (Ewbank, 1964, 1967; Mandiki, *et al.*, 1989). In cattle with twins, the mother-young bonds are weaker resulting in calves seeking out allonursing, weaning earlier, and poorer growth than singletons (Price, *et al.*, 1984/85). These results are different from those obtained in pronghorn antelopes where there were no litter size differences in nursing behavior (Byers and Moodie, 1990). None of these studies reported intra-litter variation in body weight or milk intake for twins.

Sibling Interactions

This study presents evidence for sibling competition. One twin tended to be heavier, obtained more milk, and was the displacer more often than the other. As in previous studies with goats (Klopfer & Klopfer, 1977), evidence for maternal buffering came during the first hours post-partum; the does did not engage in nursing until both young had been born. After that mothers nursed their kids regardless to the order of arrival and without interfering after nursing had commenced, even when one kid displaced another or when both kids were fighting over teat access. Most intra-litter differences related to competition were seen during the first month of life, a time when the female should have been able to exert control over resource allocation. It seems that in goats maternal buffering occurs only early in the life of kids, later

kid's aggressiveness and competition between siblings determine the nature of suckling behavior.

There is scant evidence available of intra-litter competition in domestic or wild artiodactyls. In sheep, Burfening (1972) recorded an interaction between sex and litter size, where male lambs in mixed sex pairs always grew larger than females and than males in same-sex litters. Price *et al.* (1984/85) found in a study of free-ranging cattle that one twin was more adept at milk stealing than the other, which stayed suckling the mother more. It is not known which was the heavier calf or the sex of the calves. Studies of intra-litter competition in wild ungulates and feral domesticates are necessary to characterize the nature of parent-young interactions more fully.

Control of Resources

The effect of sibling competition on nursing and mother-young interactions, and the observation that sex differences in nursing were most evident in kid behaviors, and not in maternal behavior suggest that kids were an active participant in controlling the allocation of resources. Does sometimes tried to avoid nursing and avoided the kids; the kids responded by pursuing the female and often blocked the female's path until she stood and nursing commenced. The few studies reported that describe the role of the young in the procurement of resources suggest that the allocation of resources in ungulates is not completely under the control of adult females. For example, lambs have different strategies for approaching an ewe for nursing; if it is their mother they adopt a frontal approach and if it is an alien ewe, they approach from rear or side (Poindron, 1976). Similarly, water buffalo calves are active and successful solicitors of milk from their mothers and alien cows, and use a variety of approach behaviors when dealing with either. They follow a strategy of maximizing the total number of solicitations rather than the probability of success (Murphey, Paranhos da Costa, de Souza Lima, & de Moura Duarte, 1991; Murphey, Paranhos da Costa, Gomes da Silva, & de Souza, 1995). These imply that selection processes have acted during ontogeny to produce young with flexible behavioral strategies to obtain milk. Whether individuals have different strategies or one, and the relative benefits and costs of each has not been studied in any detail.

Byers and Moodie (1990) argued that in those wild ungulates that show male bias in provisioning during lactation growth rate is slow, and females are likely to be able to produce enough milk to invest extra on

males; whereas in species with high growth rates the mothers can not show provisioning biases during lactation. To this we would like to add litter size as an intervening variable. Oftedal (1985) argued that species that twin regularly have high costs of lactation, and thus male-biased nursing would likely be seen in singletons and not in twin litters. Most of the ungulates in which there are no sex differences in nursing behavior or growth during lactation are species that twin regularly (see Byers & Moodie, 1990). The lack of sex differences could be caused by a combination of limits in milk availability for twins, and the inability of mothers to control allocation of milk among their precocial young. For sexually dimorphic species, if males are not getting more milk than females, they must procure more food elsewhere either as milk theft or foraging, have more efficient digestion and conversion of food to weight, or expend less energy than females. These suggest that there is strong selection for specific traits of young males that enable them to obtain more resources. The active role of offspring is likely to be an important determinant of parental resource allocation in precocial species with multiple offspring.

The results of this study should be replicated under more naturalistic conditions than corraled dairy goats, or a captive study with more twin litters of same sex and mixed-sex, as well as triplets. Our sample may have been inadequate to detect small differences between sexes or litter size. Domestic ruminants are a good model to study these problems because breeds differ significantly in lactation curves, litter size, growth rates, temperament, and adult body size among others (Frisch & Vercoe, 1978; Gipson & Gorssman, 1990; Hohenboken, 1986; Plasse, 1978). Future studies should compare low milk yield goats with high milk yield breeds under different nutritional regimes.

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ANIMAL COGNITION IN RELATION TO FARM ANIMAL WELFARE: THE NEED FOR A DIFFERENT APPROACH

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ABSTRACT: Reviewing various ideas about animal cognition, including the radically different approach developed by Maturana and Varela (1987), brings to light serious concerns about the ability of the current science of cognitive ethology to address issues of animal welfare or to provide useful interpretations of animal thinking and awareness. The proposition that farm animal welfare will be properly assessed only when much more is known about the cognitive abilities of the animals concerned is critically discussed. This principle is supported, but the current means of achieving it are questioned. It is argued that a broader scientific basis is needed to enhance a cognitive ethology that is merely an additive combination of behavioural observation and information-processing models of cognition.

INTRODUCTION

In recent years many scientists have said that the study of animal welfare in farm production systems requires a better understanding of cognitive processes (e.g. Curtis and Stricklin, 1991; Duncan, 1996). In fact Duncan and Petherick (1991) argued that animal welfare depends solely on the "cognitive needs" of the animals concerned and that, if these are met, most physical needs are also protected. The broad relationship between cognitive ethology and animal welfare was reviewed by Bekoff (1994). Several authors have canvassed the significance for animal welfare of the possibility, or probability, that animals conceive ideas, think about objects or events that are not part of their immediate situation or consciously formulate plans that will direct their future behaviour (e.g. Rogers, 1994; 1997). At the same time the burgeoning field of cognitive science has opened up many lines of

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investigation.

The broad sense in which pioneers like Griffin (1976; 1984; 1992) spoke of animal cognition - animal thinking - animal minds - spawns many fascinating lines of enquiry, but also invites criticism. Kennedy (1992) argued strongly against involving cognitive processes in causal mechanisms of behaviour calling it "resurgent anthropomorphism" and denying that the more sophisticated information processing models which are available in cognitive science today make cognition any more acceptable in ethology. He also warned against our predisposition to attribute intention and purpose to other people and animals which McFarland (1989) had called the "teleological imperative." They argued that attributing intentionality is a case of putting the ultimate cause onto the proximate cause of behaviour.

Where does cognition fit in the complex web of explanations about animal consciousness, subjective experience and welfare? By examining various uses of the term, cognition, including the radically different approach initiated by Maturana and Varela (1980; 1987), I hope to shed some new light on the study of animal cognition in the context of farm animal welfare. The literature on cognition in the human behavioural sciences, including the extensive neurophysiology involved, is beyond the scope of this paper, but some principles will be mentioned where appropriate.

THE HISTORY OF COGNITION IN ANIMAL ETHOLOGY

In animal ethology there has been considerable debate about where cognition fits in. In its very early days the causes of behaviour were studied in terms of purposive, instinct-driven mechanisms, this being regarded as a more scientific approach than the earlier culture of animal mentalism. In the first half of this century there was a profound swing to the reflex behaviourist tradition, originally led by Watson and stimulated by the publication of Pavlov's work, in which the animal's mental processing was not considered at all. There were exceptions to this such as the work of Köhler (1925) on the mentality of apes in which the idea of insight was introduced. The founders of modern ethology, Lorenz and Tinbergen, did not bring in cognition, but they opened the science for the second half of this century to the study of functional as well as causal explanations of behaviour. There has been increasing use of cognitive interpretations of animal behaviour generally in the last 20 years, but the most overt cognitivism is found in

behavioural ecology and comparative psychology where functional explanations are most widely used.

One of the fathers of the modern cognitive approach to ethology was Tolman (1932) who stated that he was not a mentalist, but a behaviourist; that his system was purposive, but not anthropomorphic. This distinction figures prominently in the subsequent debates about cognition. Tolman maintained that acts of behaviour have distinctive properties of their own which cannot be reduced to their physiological mechanism, a line of thought which is akin to an old idea known as *entelechy* or to the notion of emergent properties in systems theory today. He introduced the concept of cognitive maps, whereby animals acquire and store information about their surroundings, for the purpose of using it in their future behaviour.

Some modern protagonists of animal cognition (e.g. Griffin, 1984; Wilder, 1990) have predicted that we should soon be able to explain the subjective mental experiences of animals, including feelings and intentions, but they appear to be using the term cognition to encompass a wider spectrum of conscious thought and knowledge than is generally addressed by the information processing models which occupy centre stage in cognitive science today. Others such as Staddon (1989) called this approach a needless complexification, while at the same time they freely use functional explanations of so-called purposive behaviour in intentional systems. Kennedy (1992) warned that cognitivism, focusing on the internal representation of knowledge - expectancies, images, intentions, goals, plans, etc. - had the hallmarks of a return to anthropomorphism.

A typical summary of this dilemma (e.g. McFarland, 1985) is that cognition refers to the mental processes that we cannot observe directly in animals, but for which we have some indirect scientific evidence. In this sense, cognition arises in the context of learning, where it is generally agreed that there is a spectrum of learning ability ranging from the most simple cases, e.g. in lower species, or Pavlovian conditioning, through to the complex cognitive ability of humans. Since cognition involves learning and thinking processes which are not directly visible, we must rely on indirect evidence to decide where on this spectrum of learning ability a particular animal lies. Thus there have been "hidden" aspects of simple conditioning revealed to be examples of "associative learning." The central issue in contemporary learning theory (Dickinson, 1980) is the idea of internal representations or mental images. Whether it is a declarative representation (mental image) or a procedural representation (set of instructions), this

cognitive process is what guides future behaviour, though (by definition) this is not regarded as intentional in the case of a procedural representation.

To the extent that it guides future behaviour, cognition must also be considered in the context of motivation theory. This has its origin in the concept of homeostasis and the idea that homeostatic requirements place behavioural demands upon animals through a feedback loop. When the internal state changes, a drive builds up which gives rise to appetitive behaviour (searching) and consummatory behaviour (satisfying the internal state). The term "drive" has been largely superseded by terms such as "motivational state." This figures in explanations of causal mechanisms, explaining why the same stimulus can produce different responses, and in functional explanations whereby beneficial consequences are achieved.

By definition, motivational state is a state of the nervous system. It is what determines the likelihood that an animal will engage in a behaviour or the strength of its tendency to do so. It describes the forces acting on or within the organism to initiate and direct behaviour towards a goal and it explains differences in the intensity of that behaviour. Toates (e.g. 1980) and McFarland (e.g. 1985) showed how models based on classical control theory could be used to explain such motivational systems as feeding, drinking, sexual behaviour and fear. McFarland developed a complex state-space approach to this type of modelling which seems to accommodate his concern that we should not attribute purpose where there is not necessarily a purpose in the terms of the animal's world (McFarland, 1989). The claimed advantage of the state-space approach was that the combined effects of both internal and external stimuli could be represented along with greater complexity of the physiological state.

A synthesis of various ethological and psychological models of motivation by Toates and Jensen (1991) showed that different models emphasise different aspects of internal or external control and therefore attach more or less importance to the question of whether animals have specific behavioural "needs." Friend (1989) and others have revived concern about the significance for animal welfare if behavioural needs are thwarted in some way. Those behaviours which seem to have primarily endogenous motivation or which increase abnormally if denied and those situations in which displacement activities occur or animals will work to be able to perform certain behaviours have been the focus of attention. Jensen and Toates (1993) said that this should not be generalised; although if one knows the environmental context a

behaviour may be called a need in a specific situation. Poole (1992) discussed the evolution of behavioural needs and distinguished between psychological needs and ethological needs.

Dawkins (e.g. 1990) developed the related idea that the cost an animal is prepared to pay for the opportunity to perform a behaviour, or to avoid something unpleasant (see Rushen, 1986), indicates the importance of that behaviour to the animal. This does not mean cost in terms of biological fitness, but cost in terms of the animal's perception at that point in time. The cost can be measured by various means, mainly preference testing and operant conditioning, e.g. by offering choices or training to gain a reward, then making the animal work harder to achieve this. The slope of the demand curve can be used as a measure of the motivational strength. Despite many obvious difficulties which have been canvassed (see Dawkins, 1990), this approach has gained wide acceptance along with Dawkins (1988) contention that behavioural deprivation is a central issue in animal welfare.

She maintained that the unpleasant subjective feelings of an animal constitute its suffering and that the key to recognising suffering is to find out how strongly the animal is motivated to do something. Her stated aim is to look scientifically at subjective experience, "from the animal's point of view," which implies that the animal's awareness of its suffering is reflected in its behaviour in a choice test or operant conditioning situation. The central issue here is the ability of the animal to act with purpose, as we understand it, or to possess an understanding of its situation which includes at least some of the same parameters which we are using to assess this situation.

The difficulty is that the purpose might be only in our minds. There have been many deep and far-reaching analyses of this problem which will not be discussed here. Dennett's analysis (see Dennett, 1991) of intentional systems with different orders (levels of complexity) which can be distinguished empirically has been considered favourably in an ethological context (e.g. McFarland, 1985). Many related questions about the possibility of self-awareness in animals and whether consciousness is a necessary prerequisite for suffering will be left aside here, but they have been discussed elsewhere (e.g. see Bekoff, 1994).

It is apparent in all these discussions that the idea of awareness or understanding is not purely concerned with mental experience, but also embraces the emotional experiences of animals. Emotion in human experience is said to have subjective, physiological and behavioural

manifestations. At one level it is an intensely private experience, but at the physiological level there are autonomic nervous responses, for example, which are clearly defined. This physiological emotional arousal is very similar whatever the arousing stimulus may be, although humans can reflect on these responses differently in the process of describing their feelings. In comparative psychology a continuum is described through conation, cognition, affect to self-awareness. Thus subjective feelings are considered to refer to the self-awareness of affect (Salzen, 1989). In dealing with what we perceive to be an animal's awareness of its affect or its emotions we are also dealing with our awareness of our affect in this situation. The need to clarify the distinctions and the connections between mental and emotional experience is one of the major challenges we face in considering cognition in animal ethology.

COGNITIVE ETHOLOGY TODAY

Cognitive ethologists tend to give mental state priority over the physical state of the animal, while also including the emotions. Duncan and Petherick (1991) held that the animal's mental state is crucial to its welfare. Duncan (1996) maintained that the animal's "feelings, emotions or affective subjective states" were "cognitive representations of their needs" and that the concept of welfare could only be applied to sentient animals, i.e. those capable of feeling. Bekoff (1994) also considered sentience to be a central issue and said that cognitive ethologists are interested in comparing thought processes, consciousness, beliefs and rationality in animals by a broad spectrum of natural behavioural observation, with particular emphasis on individual animal characteristics. The challenge is to understand the way in which animals perceive their environment. Perception of the environment is almost invariably described in terms of information and it is the processing of that information by the central nervous system which has been the main focus of attention.

Duncan and Petherick (1991) considered an animal to be aware of stimuli through both its feelings (for internal events) and its perception (for external events). A feeling is a specific activity or process of a sensory system of which an animal is aware and it is part of the animal's emotions (Duncan, 1996). A higher level of cognitive processes consists of memory and learning which they said are more likely to involve neural network reorganisation (dispositions to form

particular connections) rather than the storage of information per se; a point which has been amply supported by more recent developments in cognitive science (see next section). Duncan and Petherick (1991) acknowledged that conclusions about an aspect of suffering such as fear or frustration are based on an interpretation of behavioural responses without directly answering the question of whether the animal is aware of unpleasant feelings. The finding that chickens will learn a procedure "to avoid being frightened" was taken as evidence that the birds had suffered an unpleasant mental experience.

Phillips and Piggins (1992) gave an interesting overview of research on the perception of the environment by farm animals which summarises the mainstream approach, i.e. that the animal acquires information ("that which reduces uncertainty") from its environment. They distinguished between sensation, perception and cognition while also considering these to be overlapping terms. Sensation is the initial processing of this information by transducers and their immediate neural connections. Perception is an awareness of that information as a pattern or in a context which is a physiological substrate. Cognition refers to the inference or meaning which the stimulus has and thus involves some degree of memory. They describe this as a spectrum of increasing complexity of both event and purpose occurring at progressively higher levels of the brain.

These authors (Phillips and Piggins, 1992) also differentiated three appropriate methods of study for these phenomena: physiological, psychophysical and ethological. In the first case they refer to conventional neurophysiology; in the second they speak of interpreting the relationship between stimulus and response as in experimental psychology (e.g. operant conditioning), in which environmental variables are strictly controlled; while the third case is non-intrusive behavioural observation under natural conditions. Each of these methods is currently being employed in studies of farm animal welfare and considerable detail has been accumulated, but the explanation of these perceptual phenomena in cognitive ethology and their implications for animal welfare are far from clear. There is a body of neurophysiological and behavioural evidence about the ways in which farm animals use their visual (Entsu *et al.*, 1992; Piggins, 1992), auditory (Heffner and Heffner, 1992) and olfactory (Perry 1992) sensory processes (Kendrick, 1992) and also their tactile receptors, particularly in relation to the perception of pain (Livingston *et al.*, 1992).

With a view to understanding the significance of cognitive

processes in farm animals, the pioneering work of Kendrick (1992) warrants close attention. He considered that cognition refers to the mental facility of knowing, which includes knowledge about objects and individuals in its environment and knowledge about itself. At a higher level it includes a knowledge of association and context and, at the highest level, the capacity to see this from another individual's point of view, which he said has only been clearly demonstrated to occur in primates. Like others previously mentioned, Kendrick maintained that we cannot assess the mental health of animals unless we can understand their cognitive behaviour.

Kendrick and Baldwin (e.g. 1987) appear to be the only people to have undertaken detailed neurophysiological studies of cognitive processes in farm animals (see Kendrick, (1991; 1992). They studied the activity of single neurones in the temporal cortex of the brain of conscious sheep to investigate the process whereby this animal recognises other animals and humans and various types of food. The involvement of the temporal cortex of sheep in visual processes was clearly shown. The importance of specific visual features such as horns on faces was demonstrated and it was concluded that sheep (and probably other farm animals) possess a specialised neural circuitry for the recognition of other individuals and objects which is similar to that of primates. Kendrick (1991) commented on the importance of social learning and previous experience on the brain responses. Kendrick (1992) emphasised the finding that the activity of visual recognition cells is clearly influenced by the emotional or behavioural significance of what is seen, e.g. favourite foods are more potent stimuli than are less preferred foods, etc.

Kendrick (1992) regarded the visual information processing as being "coded more on the basis of similar emotional/behavioural significance to the animal than on the basis of physical similarity." This author concluded, as a principle of cognitive behaviour, that the neural processing mechanism for recognition of individuals and objects was inextricably linked to the brain centres which are involved in emotional behaviour and memory saying that: "it is impossible for an animal to identify an individual independently from experiencing the emotional/behavioural significance that it has. As such we should not regard sensation and emotion as separate systems, but as an integrated continuum." He considered this remarkable influence of context, learning and motivation on an animal's sensory analysis system to be proof that animals have a conscious interaction with their environment, not merely a response mechanism.

This author also mentioned that temporal cortex cells responding to food or faces sometimes continue to show changed activity even in the absence of these stimuli (Kendrick, 1992). In my opinion he has shown that, while it is possible to demonstrate stimulus-specific activity in brain cells, much of this activity appears to be state-dependent rather than stimulus-dependent. In other words it is the internal organisation of the neural network that mainly determines its activity in the course of the animal's perception of its environment. This parallels closely other developments in cognitive science which will be described in the next section.

A further interesting development of the link between emotional and mental experience in the context of farm animal welfare is the idea of the "emotional brain" (Simonov, 1986) which has been elaborated by Wiepkema and Koolhaas (1992). This is essentially a neural information-processing model in which emotions are considered to be brain activities whereby animals assess their actual state and possibilities on the basis of their previous experience and present information. Thus the brain enables animals to detect order in their world by constructing cognitive maps and to predict and control it, but this is fundamentally an emotional experience depending on the degree of predictability and control which arises in this appraisal process.

This approach makes it possible to define stress as a state of the animal resulting from a significant decrease in predictability or control. Changes in certainty arising from the neural processing of information are accompanied by the expression of emotions (Wiepkema, 1990) and a decrease in certainty results in an unpleasant emotional experience. The underlying emotional state ranging between fear and pleasure was said to give meaning to questions about welfare and to be instrumental in guiding subsequent behavioural adaptation. Wiepkema and Koolhaas (1993) summed up this approach saying that: "individual vertebrates give great priority to those activities that promote and maintain a *reliable grip* on their actual life conditions" (emphasis added). They also said that when individuals "loose grip on their life conditions stress symptoms appear and their welfare becomes problematic." This also has parallels in modern cognitive science.

None of these approaches in cognitive ethology today can be said to deal effectively with the basic issue of the "mind-body split", the separation of mental from physical states, nor do they address the circularity problem mentioned at the beginning of this paper which arises from ascribing intentionality in interpreting an animal's behaviour and thereby running the risk of confusing functional with

causal aspects of behaviour (see Hinde, 1982; Kennedy, 1992). The cognitive ethology implied by these approaches is simply an additive combination of behavioural observation and an information-processing model of cognition.

SOME DEVELOPMENTS IN COGNITIVE SCIENCE

The historical development of cognitive science is too complex to review thoroughly here, but there have been certain crucial changes which may provide opportunities for a different approach to the study of animal cognition. My very brief interpretation of these changes follows that of Varela (1979; Varela *et al.*, 1991), Ceruti (1994) and Mingers (1995). The transmission of information, from the outside of the animal to its inside, was the major thread in the early stages of cognitive science. By the mid 1950's the computational approach to cognition had become widespread. Essentially cognition referred to the neural processing of information which provided an internal representation of the external environment, e.g. specific neurones in the visual cortex responding to edges and movement etc. This remains the most prevalent view of cognition in the applied sciences such as animal ethology today.

From the 1970's onwards, however, increasing attention has been given to the self-organising properties which arise from the rich network of connections in the central nervous system. In this case cognition was seen to embrace a more complex form of processing environmental information from which something new may arise, i.e. an emergent property, according to its operation as a self-organising system. Edelman's (1992) "neural Darwinism", which he hailed as "the beginning of the neuroscientific revolution", referred to the selective optimisation of this self-organising process, thus giving cognition an evolutionary perspective. In this scenario the idea of the outside as an absolute reference point still existed, but it had diminished in importance.

Meanwhile, the advent of second-order cybernetics (see Varela, 1979; Ceruti, 1994), against a backdrop of post-modern philosophy in which the foundations of absolute knowledge were being questioned, purported to do away with the idea of internal cognitive representations altogether. In this view the cognitive process was said to be "bringing forth" the regularities, not detecting them; the rich network was regarded as capable of constructing order through its interaction or

connection with its surrounding medium. Every sensory operation is a pro-active, two-way, cognitive process of coupling between animal and environment. Every change in the animal's nervous system is associated with a corresponding point of change in its perceived environment. This process was termed "enaction" (Varela *et al.*, 1991).

Therefore there are three distinctly different approaches to cognitive science which co-exist at the present time. They may be summarised as (1) cognitivism (or information processing), (2) connectionism (or emergent properties) and (3) enaction (the model based on second-order cybernetics). The first two agree on the centrality of representation, but differ on how it occurs, while the third approach disagrees that representation is the essence of the workings of the mind. Instead a history of two-way connection, without information being collected or representations being made, is the basis for the cognitive state of the animal at any point in time.

The first approach is the one which holds sway in the mainstream of research on cognitive ethology and in discussions of animal welfare. The more advanced connectionist model of cognition, with emergent properties channelled by Darwinian selection principles, has come into use in behavioural ecology where functional explanations predominate. The current strong emphasis on evolutionary adaptation in explanations of behaviour tends to favour the increased use of complex computational models of cognition. The third approach has not yet been considered in cognitive ethology, probably because it is a more radical development which is still controversial even within cognitive science.

The relevance of the enaction model of cognition to cognitive ethology lies firstly in its ability to deal with the problem of circularity. This is what sets second-order cybernetics apart from other explanatory frameworks. In the enaction model, cognition is circular by nature and its results arise as a self-organising system, not as a result of a linear sequence of events. The system is described, not by its constituent parts, nor by a beginning and an end, but in terms of its circularity.

Further consideration of its biological basis may be helpful. Maturana and Varela (1980; 1987) coined the term "autopoiesis" to describe the self-producing and self-referring property which they said characterises the operation of all living things. They developed the first systemic definition of living systems based on second-order cybernetics claiming that this provided a theoretical framework for addressing the relationship between a system's form and its behaviour. Thus a cognitive system was defined as "a system whose organisation defines a

domain of interactions in which it can act with relevance to the maintenance of the system itself" and the process of cognition is the acting or behaving in this domain (Maturana and Varela, 1987).

The mathematical foundations of circular systems are quite different from those applied to linear systems (see Varela, 1979). A system which computes its own organisation, as in the autopoietic nature of living things, also has the systemic property of "operational closure" which means that it can only deal in variations on what it already is; it cannot add anything from outside.

If we regard our animals in this way, then their interactions with the environment could never be instructive, i.e. consisting of external, unambiguous information. Instead environmental changes are non-specific triggers for change in the animal. The operation that results from the trigger is determined solely by the internal state of the animal at the time of the interaction. Maturana and Varela (1987) described the operation of the nervous system as operationally closed and totally state-dependent rather than stimulus-dependent. The findings of Kendrick (1992) on visual perception in sheep reviewed earlier are not inconsistent with this explanation even though they were interpreted using a different model.

Of course it is well known in ethology that the internal state can modulate the response to external stimuli, but in the enaction model the internal state is the sole determinant of the nature of the "response" which means that objects and events need to be examined for their connectability or perceivability rather than for their information content.

Maturana and Varela (1987) described the "structural coupling" of the animal with the environment at any moment as the mechanism which, by continuing recursion, determines the cognitive state of the animal and the course of its physiological and behavioural adaptation. The explanation of Wiepkema and Koolhaas (1992) of emotions generated in the brain, although it is an information-processing model, appears to have a good deal of agreement with this when it refers to the animal's need to "maintain a reliable grip" on its living conditions.

The enaction model of cognition also appears to have relevance for cognitive ethology in that it makes the cognitive state of an animal a more direct reflection of its observed behaviour without the necessity to speculate about the animal's motivations or memory or "top level" cognitive processes. The idea of the "embodied mind" (e.g. Varela *et al.*, 1991) attempts to restore the mind-body split and does not give the animal's mental state priority over its physical state as has been the case

in most reported studies of animal cognition.

IMPLICATIONS FOR COGNITIVE ETHOLOGY

There is inevitably some overlap between the causal, ontogenetic, functional and evolutionary aspects of ethology. The original classification by Tinbergen of these four types of question has contributed greatly to the development of ethology, but it can also create difficulties such as the circularity already mentioned (Hinde, 1982; Kennedy, 1992). Kennedy (1992) argued strongly against introducing cognitive processes at the top level of a hierarchy of causal mechanisms because he said it broke the coherence of the study of causation of behaviour.

Whether to attribute intention or purpose to the behaviour of animals has always been a vexed question. There is a good argument that to do this should help us to understand the behaviour as a whole, but if we fail to acknowledge the teleological confusion about function and different types of causation, we could be restricting opportunities for further scientific progress. Similarly, it is commonly stated that beneficial consequences should be referred to as functions which is to say that purposive means the same as adaptive. Once again there is a danger of being locked into a closed loop without acknowledging it.

Advocates of cognitive ethology such as Bekoff (1994) claim that it can inform wide-ranging issues such as consciousness, intentionality, self-awareness and the social and perceptual worlds of animals without saying how this is to be achieved. While I agree wholeheartedly with the stated advantages of enlarging our interpretation of behaviour to include cognitive issues, I doubt that the difficult questions can be answered while the circularity of the argument is not fully acknowledged.

Writing on conceptual and biological aspects of stress, one of the pioneers of the use of systems theory to explain behaviour, openly acknowledges that the best definitions and models of stress which are available at present do not escape the criticism of being essentially circular (Toates, 1995). Discussion about stress and welfare has been blessed and bedevilled by circularity of this kind. For example, a rise in glucocorticoids in the animal's blood stream is both a sign that the animal has been stressed and an indication of its ability to cope successfully with its environment. Stressors are obviously more than simply inputs to the system and stress is more than just the outcome

that results from them. It is more of a bi-directional engagement such as was proposed in a "transactional model of stress" by Cox and others (see Toates, 1995).

In the enaction model of cognition there is no input-output, no first-order causal relationship between stimulus and response, and no information processing. Instead, what the animal perceives depends on how its internal organisation can connect with its outside world at that point in time. It does not depend on the nature of the external stimulus and is not defined externally, although often it may appear that way because of a particular history of coupling which has produced a particular internal state that we denote as a certain knowledge of the environment.

A cognitive animal is sometimes described as a thinking animal; where cognition is said to refer to the use of "internal mental operations in generating specific behavioural responses to sets of external stimuli" (Real, 1993). Thinking is just a word we use to describe something we have inferred from our observations, but it does not explain how or what an animal perceives? The alternative suggested by modern cognitive science is not to consider that animals process information or have specific knowledge of anything outside themselves, but to consider each "stimulus-response" situation as a connection between the animal and its environment and to examine the history of such connections. The idea is that the "meaning" of any object or event, "from the animal's point of view", may be revealed more clearly in the history of these connections.

The current way of dealing with this as a higher level cognitive process is to invoke the idea of memory. This is a word we use to represent certain changes in internal state that have resulted from the animal's previous experience, but its direct measurement is still questionable; it must be inferred from other observations of behaviour. The neural organisation of memory and emotions was reviewed by LeDoux (1993) whose work has gone a considerable way towards establishing the existence of emotional memory systems in the brain. These are still not clearly defined, however, and even if they were, they are seen as storage houses for external inputs, so their ramifications for subsequent behaviour still have to be explained as well. Similar gaps exist in our understanding of learning. Despite a huge literature and body of theory on how learning occurs we still rely on indirect assessment of it and we have had to develop a very elaborate theoretical framework in order to interpret behavioural or physiological data.

Second-order cybernetics offers no easy solution and is not an

alternative paradigm to the present understanding of memory, learning and cognition. It simply provides an additional set of tools that may be helpful, particularly in studies of animal welfare. In a society which is more familiar and more comfortable with the idea of manipulating controllable systems than with the idea of understanding self-organising systems it is unlikely that second-order cybernetics or the enaction model of cognition will replace the better known theoretical frameworks, nor should it. It may add another dimension to the examination of these very complex subjects.

At the very least it implies that caution is warranted in attributing animal responses to external stimuli at any point in time without having a detailed knowledge of that animal's previous experience. An analysis based on the so-called "information" contained in any particular object or event is not the only way of interpreting animal behaviour in a cognitive sense for the purpose of assessing its welfare. Too often we seem to regard the objects and events of the environment as the causes of stress or welfare problems. But, as Duncan and Petherick (1991) and others have pointed out, it is the awareness of the animal which is critical; what would be stressful in one case might not be in a different situation.

An example of the way in which the explanatory framework affects the interpretation of behavioural observations is in the use of preference testing. These are usually interpreted as if the animal has made a choice, conscious or otherwise, but the results often raise doubts about whether animals do know what is best for them, particularly in the longer term and what other factors influence the apparent decision (see Dawkins 1990). Grandin (1994) was concerned that previous experience can affect choices and she presented evidence that the reluctance of cattle to change a learned choice may confound the results of preference testing. If the enaction model of cognition is used it is far more important to know the precise cognitive history of each individual animal than to be concerned with the supposed nature of the choices offered.

It may not be sufficient to call this, as Dawkins (1990) has done, the animal's awareness of its suffering that is reflected in its behaviour in a choice situation; it is the animal's entire history – its cognitive ontogeny. This approach questions the necessity of invoking the idea of conscious choice in our explanation of this process. Conscious choice is essentially a post hoc analysis of the situation when the alternatives have become known. The animal could be predisposed to act differently as a result of cognitive processes ensuing from its

previous experience, but this could be achieved by connecting differently with its environment – being aware of different features – rather than by weighing up any alternatives at the time of the action.

The debate about stimulus specificity or stimulus generalisation (e.g. the ability of farm animals to discriminate between people, see de Passillé *et al.*, 1996) provides another example of the influence which the particular theory of cognition has on the interpretation of behaviour. It has proved very difficult to demonstrate that a particular response is stimulus specific or that responses to stimuli become more generalised over time. Using the enaction model one would be attempting to relate the particular response to the history of contacts, not to the nature of the stimulus itself.

IMPLICATIONS FOR FARM ANIMAL WELFARE

The mechanism by which animal welfare issues are researched and discussed and community decisions are made involves human cognitive processes in providing satisfactory explanations of the processes of animal cognition. The circularity which is inherent in this operation has often caused problems. There are elegant ways of addressing the problems such as the incorporation of human values into the discussion so that different levels of concept are defined and animal welfare can be regarded as a “type 3” concept which cannot be measured in an entirely objective way (Fraser, 1995). Whatever device is used there is a self-organising property inherent in the animal welfare debate which may be easier to manage if it were more openly acknowledged.

The whole issue of animal welfare can be described as a self-organising system because the enaction model of cognition can also be applied to the human conduct of cognitive ethology. It is something of a blind spot that we tend not to examine what it is that we are doing when we make our explanations of cognitive ethology. The application of second-order cybernetics to human communication and understanding is further discussed by Fell and Russell (1994). A particular animal welfare issue arises and is defined in our conversation, i.e. in the language we use. It may be solved eventually in precisely the same way when someone provides a satisfying explanation for how the animal is expressing itself in that situation. This process has the properties of coupling, recursion, closure and circularity that can be clearly defined only by second-order cybernetics.

It is likely that new measurements as well as new interpretations

will be needed to further the application of cognitive science to complex farm animal issues. Evidence is accumulating rapidly that the way animals perceive their environment is reflected in their immune system (Husband, 1995) and so measures of immune competence are assuming increasing importance (e.g. Skandakumar *et al.*, 1995). There are some prominent immunologists who, although in a minority, have persisted for many years in choosing to explain immune responses as part of a cognitive system (e.g. Vaz and Varela, 1978; Vaz and Carvalho, 1994). There is a somewhat controversial, but well-developed theory in which the immune system is seen as a part of the mind (Booth and Ashbridge, 1993). This points the way to a considerable broadening of the concept of cognition and the conceptual framework that we use to explain and understand animal welfare.

Measurements of complex behaviour in sheep such as the approach-avoidance test of Fell and Shutt (1989) and Fell *et al.* (1991) have been related to the animal's motivational state and to immune function (Gates *et al.*, 1991), but have not yet been applied to animal welfare decisions. This test pits the natural flocking ability of sheep against their natural flight distance or fear of humans by placing them in a specially designed arena that has sheep in view at one end and a person standing in front of the sheep. The way the test animals behave can be interpreted as a result of their learning (conditioning), their memory, and/or their psycho-physical (cognitive) state at that point in time.

The enaction model of cognition attempts to avoid splitting off higher-order processes (such as the processing and storage of what we interpret as information and the resultant intentions) from the rest of the animal. The approach-avoidance test mentioned above provides a readily quantifiable assessment of the state of the animal when it is put into a situation that requires it to "think" (that makes certain specific sensory connections available) and therefore is more likely to reveal its true condition. Its behaviour is seen to be revealing what it "knows" about its world at that point in time. These measurements coupled with a detailed dossier of the animal's history (and especially if neurophysiological measurements can be added) provide a basis for a richer, less subjective, assessment of the animal's welfare. A more complete review of this testing procedure is being prepared for publication.

Much effort is currently being put into the testing of farm animals for "temperament" (see review of individual differences by Manteca and Deag, 1993) or measurement of their fear reactions to different

stimuli in various behavioural test situations (e.g. Boissy and Bouissou, 1995), but the interpretation of fearfulness as an “underlying psychobiological profile” is not universally accepted because not everyone agrees that fear can be described as a unitary phenomenon (see review by Boissy, 1995). This is another example of the difficulty of interpreting behavioural tests within existing models of cognition, particularly with reference to animal welfare.

Duncan and Petherick (1991) concluded that effects of management on animal welfare will be properly assessed only when very much more is known about the cognitive abilities of the animals concerned. My conclusion is that the concepts which have been reviewed here support their statement, but show also that this line of inquiry is fraught with difficulty and suggest that we will need to explore different approaches to the study of animal cognition in order to maximise our opportunities for progress.

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MAKING PLACE FOR A COMPARATIVE SCIENTIST: ROBERT MEARNS YERKES AT HARVARD, 1902-1917

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ABSTRACT: During the first decade of this century, Robert Mearns Yerkes struggled to make a place for himself within Harvard University's Division of Philosophy as a comparative scientist. From the perspective of a young assistant professor, Yerkes' diary and letters permit a glimpse into the all-too familiar struggle of establishing career and family.

Comparative psychology at the turn of the twentieth century was a relatively new discipline in the United States. The idea of combining psychology and biology into a single domain of study was foreign to many and few such researchers existed. Robert Mearns Yerkes. Yerkes, who preferred being called a "psychobiologist" rather than a "psychologist" (e.g., Yerkes, 1932), focused his talent on advancing the comparative, psychological study of animals, on bridging the chasm between psychological and biological science, and on developing and promoting objective methodology (Yerkes, 1950).

When Yerkes entered Harvard in the fall of 1887, he entered as a special undergraduate. He applied to Harvard to study medicine but was denied admission because Harvard did not then recognize the bachelor of arts degree Yerkes had earned the previous spring from Ursinus College in Pennsylvania. This temporary setback would lead Yerkes to psychology. Yerkes' Harvard advisor, and one of his favorite teachers, was Josiah Royce. Royce recognized Yerkes' abilities and interests. As Yerkes' undergraduate days grew to a close, Royce suggested Yerkes combine his biological, psychological, and

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philosophical interests in to the emerging area of comparative psychology. Royce offered to introduce Yerkes to Hugo Münsterberg, then charged with the direction of the Harvard psychology laboratory. At that time, and well into this century, psychology at Harvard was a component of the Division of Philosophy. Yerkes, as he relates in his unpublished autobiography, was charmed. Münsterberg received him warmly and encouraged him to give serious consideration to Royce's suggestion. Although not fully committed to this shift in plan, Yerkes entered the Harvard Graduate School in 1898.

Because no one in the Division of Philosophy was well-versed in animal psychology, Yerkes conducted most of his graduate research with Harvard's comparative zoologists—under Münsterberg's watchful eye. In March of 1902, Yerkes recorded in his diary that William James personally conducted the oral examination in comparative psychology, an exam more resembling a conversation than a test. Although Yerkes passed, James suggested Yerkes attend less to "facts" and more to the theoretical side of comparative endeavors (Yerkes, 1902). James' words would prove prophetic.

When Yerkes completed his PhD in the spring of 1902, Harvard offered him a job as a teaching fellow. Yerkes balked, and asked Münsterberg, by then Division Chair, why Harvard President Charles W. Eliot had not offered an instructorship. Unknown to Yerkes, Eliot questioned the usefulness of the appointment; he questioned a biologist among the philosophers, a goat among the philosophical sheep (see O'Donnell, 1985). Eliot's concern was well founded for at the time Yerkes usually characterized himself more a physiologist than a psychologist (e.g., Yerkes, 1930b). Münsterberg intervened, convincing Eliot that Yerkes' appointment was needed for the Division's growth, particularly if Harvard wished to stay abreast of the psychological work at other schools. Yerkes joined the Harvard faculty in 1902 as an instructor who understood his responsibilities to be research and teaching, in that order (Yerkes, 1950).

The reality of life in the academy dawned rudely on Yerkes. In May of his first academic year, while sitting on a PhD examination committee, he became disturbed when he perceived Münsterberg passing candidates though the proceedings that Yerkes thought unworthy. He commented in his diary that "it is great grief to me to feel that I cannot ful[ly] honor and love my 'Chief.' But [it]'s inevitable...sooner or later if I say, the crack must come, our principles will conflict" (Yerkes, 1903a). Despite this hint of caution, Yerkes continued to derive inspiration from Münsterberg (Yerkes, 1904b;

1932; 1950).

Yerkes' early academic endeavors found him working to prepare lectures, a task he found arduous (Yerkes, 1950), and struggling to bring his work to the attention of biologists, a task he relished and found consuming (Yerkes, 1930b). Yerkes' experimental work flourished during those early years at Harvard and ranged across a wide variety of species, including water fleas, crabs, turtles, crawfish, frogs, earthworms, and mice. Anecdotal evidence of success is suggested in an April 1904 diary entry where he mentions only two Harvard faculty members, himself and psychologist Walter Cannon, attending a private dinner at Yale in honor of Charles Sherrington (Yerkes, 1904d). Sherrington was in New Haven to give that year's Silliman Lectures, the same Silliman Lectures that spawned Sherrington's classic *The Integrative Action of the Nervous System* (Sherrington, 1906).

Throughout the summer of 1904, Yerkes became increasingly dissatisfied with his Harvard position (e.g., Yerkes, 1904h). Although he disclosed in his diary that he found Münsterberg's administrative methods unadmirable (Yerkes, 1904f), Yerkes could not conceive Münsterberg as "insincere and unreliable" (Yerkes, 1904g; see also Yerkes 1904e). Indeed, Yerkes believed their interactions suggested he was gaining respect in Münsterberg's eyes (Yerkes 1904j). That perceived respect did not translate into self-confidence. During the summer, Yerkes experienced nagging doubts about his ability to rival the intellectual work of Münsterberg or the colleague with whom Yerkes worked most closely, Edwin Holt (Yerkes, 1904i). Summer's end found Yerkes at an emotional low tide. That August, Münsterberg asked Yerkes if he would serve as a recording secretary for the International Congress of Arts and Sciences to be held the next month in St. Louis (H. Münsterberg, 1904). A vice-president of the organization, Münsterberg needed, in addition to a secretary, a liaison to negotiate the arrival and comfort of the international guests. He chose Yerkes; Yerkes accepted.

During that Congress, Yerkes committed a political error that apparently cost him Münsterberg's good will—at least momentarily. Yerkes confided in his diary that he circulated among the Congress's participants asking their opinion of Münsterberg. The two words that most frequently appeared, he recorded, were "notoriety" and "ambition" (Yerkes, 1904k). Upon returning to Cambridge, Yerkes believed that his interpersonal interaction with Münsterberg had drastically cooled (Yerkes, 1904l; 1904m). Yerkes, who was feeling uncomfortable and somewhat paranoid, thought Münsterberg unresponsive and indifferent.

unresponsive and indifferent. To Münsterberg's credit, after a period of postconference aloofness, Yerkes' diary entries suggest Münsterberg again adopted the sheltering stance one might expect a good division chair to take toward an inexperienced, unmarried, somewhat naive faculty member; the Münsterbergs even invited Yerkes to share Thanksgiving dinner that year (Yerkes, 1904n, 1904o, 1904q). Frau Münsterberg, however, was not as gracious in overlooking Yerkes' social indiscretions. Late that year, Yerkes reported she severely castigated him for his "snobbishness" (Yerkes, 1904p; 1904r).

If Münsterberg's personal support of Yerkes seemed strong, his professional support was dubious. Münsterberg's conception of psychology did not include a prominent place for animal research. To Münsterberg's way of thinking, Yerkes' work was more correctly conceived as the work of a biologist (Kuklick, 1977; H. Münsterberg, 1911; O'Donnell, 1985). Three factors forced Münsterberg to tolerate frogs and turtles in the Division: the influence of James and Royce, competition from other psychological laboratories, and Yerkes' increasing stature among psychologists and comparative scientists alike. Despite these factors, Münsterberg's professional opinions boded ill for Yerkes' Harvard career.

Any expectations Yerkes may have harbored of a rosy Harvard future appear unrealistic in light of two incidents. First, late in 1904, Münsterberg evidently told Yerkes he would be expected to supplement his salary with work outside the University—teaching summer school at Radcliffe was a possibility (Yerkes, 1904s). The money needed to marry and the money associated with career advancement were constant themes in Yerkes' diary.

Second, in the spring of 1905, when Holt, not Holt and Yerkes, received promotion to assistant professor, Yerkes was noticeably shaken (Yerkes, 1905c). The two had spent a good deal of the spring term grouching over Münsterberg (e.g., Yerkes, 1905a; 1905b). Yerkes immediately pleaded his case to Münsterberg who made two seemly incredulous rejoinders: One, he did not think Yerkes had a chance for promotion (Yerkes, 1905c). Two, he did not believe Yerkes desired promotion (Yerkes, 1905d). After a time, Münsterberg offered to show Yerkes' work to Eliot, warning nevertheless to expect nothing to come of it (Yerkes, 1905e). Nothing did.

The entire episode plunged Yerkes into a period of self-doubt. He lamented his lack of originality and new ideas, in his words "the deadlevel common placeness of my work."

(Yerkes, 1905e, see also Yerkes, 1905f; 1905g). The depression

seemed to lift when he made a July-1905 sojourn to Woods Hole where biologists heralded him as a leading investigator of animal behavior (Yerkes, 1905h).

No doubt his marriage to Ada Watterson in September gave him new vistas of concern as well. The financial responsibility of marriage weighed heavily on Yerkes. Münsterberg had informed Yerkes that the writing scientific papers did not pay well and suggested Yerkes produce pieces of popular writing in order to supplement his income. Yerkes recorded in his diary that he found the prospect of writing for dollars "degrading" (Yerkes, 1904a).

Since even as biologists Ada and I could discover no way in which I could fairly share the labor of having babies, it was agreed between us facetiously that whenever we reproduced ourselves I should produce a book. Not that we expected book royalties to provide the necessary funds for child-rearing but in token of my willingness to support additions to the family. So far as our will sufficed we lived up to our contract; when Roberta Watterson arrived, my first book was published, and David Norton's birth coincided with the appearance of the only textbook I [wrote]. (Yerkes, 1950, p. 137)

Yerkes' diary entries explicitly reveal that he associated books and articles with career advancement. He writes, "it seems almost necessary for me to publish an important book if I wish to advance in my department." (Yerkes, 1904c). In 1907, while Roberta was arriving, Yerkes did publish a classic in behavior genetics, *The Dancing Mouse*. His *Introduction to Psychology* was published in 1911.

Marriage seems to have compromised the sanctity of Yerkes' diary. Ada begins writing little notes; Robert's entries become less frequent. By April of 1907, Ada's entries are prevalent; by the end of 1907, the diary's pages are blank and forgotten. Yerkes and John B. Watson exchanged a copious correspondence as they hashed out editorial matters, both were then associated with the *Journal of Comparative Neurology and Psychology* (see Wight, 1991) and endeavored via correspondence to produce procedures designed to study animal vision. Yerkes also struck up a correspondence with Edward B. Titchener in which they discussed professional politics and paradigms.

In 1908, Yerkes was again disappointed when a prominent Bostonian and Harvard insider— whose family financially supported the University and who had taught philosophy in the Division without pay since 1903—received the promotion Yerkes believed should have been his. Yerkes was incensed and embarrassed (O'Donnell, 1985). He told

Münsterberg that Harvard's *modus operandi* was to pay its people only what circumstances dictated and that the Corporation had only another year to adjust Yerkes' salary to a living wage (Yerkes, 1908). Titchener wrote Münsterberg that Yerkes' work was the most impressive thing in Harvard's Emerson Hall (Titchener, 1908). In April of 1908, Münsterberg again brought Yerkes' petition to Eliot's attention: Eliot relented. The news, however, was not all good. A component of the argument Münsterberg apparently used to secure Yerkes' promotion was that the University should now insist that Yerkes adjust his lectures to emphasize the educational aspects of psychology (O'Donnell, 1985). Within a month, Yerkes was encouraging Watson to "get busy on the human side" (Watson, 1908). Yerkes got busy on the human side and sometime between this letter and October of the next year successfully approached the Henry Holt publishing company about writing an introductory psychology textbook (Bristol, 1909a). A contract to that effect was signed in November of 1909 (Bristol, 1909b).

Harvard's attitude toward Yerkes began to deteriorate in 1909 with the resignation of President Eliot. Although Eliot's support of comparative psychology may have been less than overwhelming, Yerkes' diary, letters, and autobiography suggest Eliot's support of Yerkes himself was warm and cordial. Yerkes contrasts his experience with Eliot, a chemist, to that with Eliot's successor, A. Lawrence Lowell, a lawyer (Yerkes, 1950). Lowell does not receive a favorable evaluation. In fact, if Eliot had remained at Harvard an additional decade, Yerkes might have stayed for the duration of his career. Yerkes believed that Lowell considered his research a financial extravagance, peripheral to the University's interests, and recalled that Lowell communicated the notion that if Yerkes wished to advance, educational psychology was the way to travel. Yerkes' account implicitly exonerates Münsterberg of any negative influence on Lowell, painting a respectful picture of "the Chief" throughout this episode.

The archival correspondence, however, suggests a different interpretation. When Yerkes balked at permitting his work to be acknowledged in Harvard's public announcements under the heading of "Philosophy," Münsterberg accused him of insubordination, declaring, if we may paraphrase and only slightly embellish, psychology would separate from philosophy over his dead body (Münsterberg, 1909). With James's death in 1910, a pillar of support for animal psychology at Harvard was removed. Münsterberg was then attempting to mold the Harvard laboratory more to his liking. Royce offered little opposition.

Writing to Lowell, Münsterberg asserted, "I have the greatest sympathy with Yerkes' successful efforts to give importance and independence to his specialty, which however I confess has so far not opened any wide perspective of knowledge but offers many interesting little facts" (our emphasis, H. Münsterberg, 1911a; also quoted in H. Münsterberg, 1911b).

The comparative researchers of Yerkes' day were striving to generate professional respect for their enterprise. John O'Donnell (1985), in his masterful book *The Origins of Behaviorism*, observes that these individuals could have adopted one of two strategies: argue (a) psychology's focus is behavior, or (b) animal psychology contributed to the study of consciousness. John Watson chose the first option; Robert Yerkes chose the second.

In a 1910 paper entitled "Psychology in its Relation to Biology," Yerkes appeared to come over to the human side by professing consciousness the object of psychological research. His argument revolved around the assessment of psychology's scientific status by twenty biological researchers. About one-half of the sample asserted that psychology is not a science. A smaller, second group asserted that if psychology utilizes introspection as its primary method, then psychology is metaphysics. A third group countered that if psychology attends to the experimental study of consciousness as it relates to the nervous system, psychology is indeed a science. Yerkes completed the article by suggesting that if psychology were to rightly aspire to the coveted status of a science, embracing objective methodology was mandatory. Comparative psychology, Yerkes concluded, had the method the rest of psychology lacked and thus the procedural foundation of science the rest of the discipline needed. The article received mixed reviews. Physiologists applauded (e.g., Herrick, 1910). Titchener (1909b), commenting on a draft of the paper, wrote that the manuscript exhibited "freshness" and "peculiar values." Watson wrote that the only common ground he observed with Yerkes was that psychology students were "rottenly trained" (Watson, 1910). Münsterberg's pen appears to have been silent.

Yerkes composed a second apology for comparative psychology: His introductory textbook. An early mention of this text appears in a November-1909 letter from Titchener shortly after Lowell conveyed the message that pedagogical work was Harvard's criterion for advancement (Yerkes, 1950) and after Münsterberg accused Yerkes of insubordination (H. Münsterberg, 1909). Titchener wrote "I look on the text-book [sic] project with mixed feelings. If the impulse is

overpoweringly strong in you, you must let it out... [however] it is thankless work, and we pay too much attention to teaching anyhow" (Titchener, 1909a). The impulse did prove overpowering; the textbook was published in less than two years.

The book's focus is introspection but its theme is a psychological system—a system ranging from plant to animal, through ontogeny and phylogeny—in which methodological considerations are paramount. With one salvo, Yerkes answered the criticisms of pedagogical and disciplinary irrelevance for the comparative approach. Harvard, however, remained unmoved. During the remaining five years of his tenure, Yerkes exercised less influence on his own campus than he did in the discipline at large. In 1916, his last year at Harvard, 14 years after beginning his academic career, Yerkes was the first and only assistant professor ever elected president of the American Psychological Association.

Yerkes' friends, the same friends who applauded the 1910 paper, were appalled at the 1911 textbook. They believed Yerkes had made introspection primary to psychology and that what was once a difference in emphasis among them was actually a foundational abyss (e.g., Herrick, 1911). Yerkes' rejoinder is interesting. In his letters, he habitually states he wrote the book for "pedagogical" reasons and that if he and his friends could briefly vacation together, each friend would find no real difference existed (e.g., Yerkes, 1911b). Indeed, the complexion of Yerkes' lifetime interests and the archival record suggest the textbook was not a student-oriented endeavor. Perhaps Yerkes had another meaning of pedagogy in mind.

The word pedagogy may refer to the act of teaching, the method of teaching, or the profession of teaching. We submit the latter was paramount in Yerkes' mind. During the early years of his career, Yerkes repeatedly attempted to sell comparative psychology and himself, struggling as an assistant professor pursuing comparative science in Harvard's Division of Philosophy: Some of his Division colleagues were not sure he should be working alongside psychologists or philosophers; he was constantly overlooked for promotion; and he worried over supporting his family. To address these difficulties, Yerkes resorted to means outside his areas of interest and research, jeopardizing his career in the eyes of some. Remuneration can take many forms. The payoff Yerkes desired most was not money but professional standing at Harvard—standing and place he was never able to earn.

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NOTES

¹ Except where noted, all letters and documents are from the Robert M. Yerkes Papers, Yale University Library, New Haven.

² The biographical information that follows is drawn from Yerkes' "Testament" (Yerkes, 1950).

³ Having recently rediscovered Mendelian genetics, this was a heady time for comparative scientists in Cambridge.

⁴ Of the three candidates, Yerkes considered only Roswell P. Angier worthy. Later that evening Angier took Yerkes to dinner during which they had a "good heart-to-heart" (Yerkes, 1903a).

⁵ In time, Frau Selma Münsterberg's opinion of Yerkes improved (see M. Münsterberg, 1922).

⁶ The bibliography, purportedly complete, that Ms. Roberta Yerkes Blanshard, Yerkes' daughter, supplied the first author lists only three popular articles during that decade. We are indebted to her gracious willingness to discuss her father. Interestingly, she still possesses the cuckoo clock the Münsterbergs gave her parents as a wedding present.

⁷ The Yerkes-Watson correspondence is housed at Yale. The Yerkes-Titchener correspondence can be found at both Yale and Cornell University.

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